Bollettino della Società Paleontologica Italiana, 51 (3), 2012, 185-191 Modena, 30 dicembre 2012

New observations on the paleodiet of the late Miocene Höwenegg (Hegau, Germany) *Hippotherium primigenium* (Mammalia, Equidae)

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KEY WORDS - Höwenegg, hipparion, mesowear, microwear, paleoecology, Miocene.

ABSTRACT - Höwenegg, a late Miocene (Vallesian, MN9) vertebrate locality in the Hegau region of Southern Germany, is known for its excellently-preserved, near-complete skeletons of various large mammals. The Höwenegg hipparion, Hippotherium primigenium *(von Meyer, 1829), is the second-most common mammal found at the site. Paleodietary assessment of the Höwenegg equid material from the collections of the natural history museums of Karlsruhe and Darmstadt, Germany, was undertaken using both light-microscope microwear and two methods of mesowear analysis. While the results of the microwear analysis suggest a grass-dominated mixed feeding diet, the mesowear analysis indicates a more browse-dominated mixed diet. The slight disparity of these results may be due to the consumption of relatively unabrasive C3-grasses, which might have concealed the grazing aspect in the mesowear signal. The disparity may also reflect seasonal dietary heterogeneity in* Hippotherium primigenium*: the mesowear signal reflects long-term dietary habits, while the microwear method records a short-term signal. While occasional fruit browsing cannot be excluded for Höwenegg* Hippotherium primigenium*, there is no clear evidence for this kind of dietary preference. This study for the first time tests a recently-proposed mesowear method on Central European hipparion material. For this method, cusp shape of maxillary cheek teeth is recorded as a single value rather than the two variables occlusal relief (high-low) and buccal apical cusp shape (sharp-round-blunt) used in most traditional approaches. The new score is, in contrast to earlier ranked-scale methods, determined by consulting a standard that comprises representative casts of seven stages in cusp shape, from high and sharp (0) to low and blunt (6) presented as a ruler. This method is shown to be less prone to observer bias then previous methods, thus providing data of higher repeatability.*

RIASSUNTO - [Nuove osservazioni sulla paleodieta di *Hippotherium primigenium* (Mammalia, Equidae) del Miocene superiore di Höwenegg (Hegau, Germania)] - *Höwenegg è una località a Vertebrati del Miocene superiore (Vallesiano, MN9) nella regione di Hegau (Germania meridionale) rinomata per aver restituito un'abbondante collezione di resti scheletrici di grandi mammiferi in connessione. L'equide tridattilo* Hippotherium primigenium *(von Meyer, 1829) è il secondo taxon più comune nella associazione raccolta a Höwenegg. In questo studio viene presentata un'analisi della paleodieta dell'equide di Höwenegg basata su reperti delle collezioni dei musei di storia naturale di Karlsruhe e Darmstadt (Germania). Lo studio è stato eseguito combinando la tecnica della osservazione della microusura al microscopio ottico, associata a due differenti metodi di analisi della mesousura delle superfici occlusali. I risultati derivanti dalle due tecniche di analisi (microusura e mesousura) risultano differenti. Mentre la prima infatti suggerirebbe una dieta mista a base principale di erbacee, quanto estrapolato dalla mesousura sembra invece indicare una dieta mista con una componente principale da brucatore. Una tale disparità nei risultati può, da un lato, essere coerente con un regime di paleodieta basata sull'accesso a piante C3 con capacità abrasiva relativamente bassa (piuttosto che a una dieta a base di piante abrasive di tipo C4), ma potrebbe altresì riflettere una variabilità stagionale nell'accesso alle risorse trofiche da parte di* Hippotherium primigenium*. Rispetto a metodi tradizionali che utilizzano la morfologia delle cuspidi espressa in variabili multiple, il nuovo metodo di studio utilizzato, basato su un approccio standardizzato combinando analisi di mesousura e microusura delle superfici occlusali, si è dimostrato più efficace e meno soggetto a errori nelle osservazioni ripetute da ricercatori diversi.*

INTRODUCTION

Höwenegg is a late Miocene (Vallesian age, MN9; Woodburne et al., 1996) site located ca. 2.5 km south of the town of Immendingen in the northern Hegau volcanic district, Germany. The locality is an extraordinary Lagerstaette that has yielded nearly fifty skeletons of fossil mammals including the hipparionine horse *Hippotherium primigenium* (von Meyer, 1829) (as the second most common mammal after the antelope *Miotragocerus*) together with abundant plant, invertebrate, and non-mammalian vertebrate remains (e.g., Tobien, 1986; Jörg & Rothausen, 1991; Bernor et al., 1997; Munk et al., 2007). The site was the subject of extensive excavation under Tobien and Jörg from 1950 until 1963 (e.g., Jörg, 1951; Tobien, 1951, 1982, 1986), and again from 2003 on as a joint project of the Natural History Museums of Karlsruhe (SMNK) and Stuttgart (SMNS) and Howard University (Heizmann et al., 2003; Munk et al., 2007).

The fossil-bearing lake bed sediments of this site have been dated ca. 10.3 Ma in age using the $^{40}Ar/^{39}Ar$ dating method (Swisher, 1996). The geomagnetic polarity (Swisher, 1996) and biochronologic correlation (Woodburne et al., 1996) of Höwenegg were shown to be consistent with the radioisotopic age. The skeletons are believed to have been deposited over a very short period of time, which suggests that the Höwenegg fauna essentially closely conforms to a biological population concept (Jörg & Rothausen, 1991; Woodburne et al., 1996; Bernor et al., 1997). The morphology of the Höwenegg hipparion has been extensively investigated by Bernor et al. (1997), and this equid was shown to preserve a number of primitive features, especially in its skull and dental morphology. Bernor et al. (1997, 2003b, 2010) have noted the close similarity of the Höwenegg hipparion to North American *Cormohipparion occidentale* (Leidy, 1856), and Bernor (2003b), Scott et al. (2005), Woodburne (2007), and Bernor & White (2010) have discussed *Hippotherium*'s

ancestral relationship to North American *Cormohipparion*. The Höwenegg hipparion in general shows a relatively gracile stature and has been demonstrated to be well-adapted to woodland environments (Bernor et al., 1988, 1997; Bernor & Armour-Chelu, 1999; Kaiser et al., 2000).

While the paleodiet of Central European *Hippotherium primigenium* and its close relatives has been addressed in several studies (Bernor et al., 1999, 2003a; Kaiser et al., 2000, 2003; Kaiser, 2003; Kaiser & Bernor, 2006), thus far only Kaiser (2003) has published results on the paleodiet of the Höwenegg *H. primigenium*. Our study will implement the mesowear and light microscope microwear methodologies.

MATERIALS AND METHODS

Material

The material investigated here consists of twelve skulls, three maxillae fragments, and five isolated teeth of the Höwenegg *Hippotherium primigenium* housed in the Staatliches Museum für Naturkunde, Karlsruhe (SMNK), and the Hessisches Landesmuseum, Darmstadt (HLMD). Not all of these specimens yielded usable data for one or both methods employed in our study (Tabs 1 and 2).

Methods

Mesowear - The mesowear method developed by Fortelius & Solounias (2000) analyzes the morphology of the paracone (or, if sharper, the metacone: cf. Kaiser & Fortelius, 2003; Kaiser & Solounias, 2003) of maxillary cheek teeth. Scored characters are the buccal apical cusp shape (sharp, round, and blunt) and the occlusal relief (high or low, depending on how high the cusp apex rises above the occlusal apex of the mesostyle between the para- and metacone) in adult individuals having normal occlusion. Kaiser & Solounias (2003) successfully extended this methodology to P4-M3 in hypsodont horses when the M2 was missing or broken, and we adopt this methodology herein. Also, recent mesowear studies commonly prefer the paracone over the metacone unless the former is damaged (e.g., Mihlbachler et al., 2011), and we likewise follow this approach here.

Mihlbachler et al. (2011, fig. S1) stated that the variables used in the extended mesowear method are not strictly independent, high-relief cusps being sharper than

Specimen number	Tooth position	Side	M. score	ad. score	Relief	Shape
HLMD Hoe 58/V1	txm2	rt	1	1	h	r
HLMD Hoe 54 (III-53)	txm2	rt	2	1.5	h	r
HLMD Hoe 488 (E55)	txm2	lt	1	1	h	r
HLMD Hoe 492 (54-F4-G1)	txm2	rt	1	1	h	r
HLMD Hoe M55/1	txm2	rt	1	1	h	r
SMNK (RLB 85/74)	txp4	rt	1	1	h	r
SMNK Hoe 8	txm1 or m2	rt	1	1	h	r
SMNK Hoe 212	txm2	lt	1	0.5	h	r
SMNK Hoe A	txm2 (metacone)	lt	2	2	h	r
SMNK Hoe B	txm2	lt	0	0	h	s
SMNK Hoe C	txm2	rt	1	0.5	h	s

Tab. 1 - Mesowear results. txm: maxillary molar; txp: maxillary premolar; rt: right; lt: left; M. score: mesowear score following Mihlbachler et al. (2011); ad. score: score adjusted as described herein; h: high; s: sharp; r: round.

Specimen number	Tooth position	Side	Scratches	Pits	Texture	Gouges	Lg. Pits	Punct. P.
HLMD Hoe 58-V1	txm2	rt	21.5	23.5	fine	no	0	no
HLMD Hoe 54 (III-53)	txm2 (metacone)	rt	12	26.5	fine/coarse	yes	0	no
HLMD Hoe 488 (E55)	txm2	lt	11.5	28	fine	no	0	no
HLMD Hoe M55-1	txm2	rt	24	26.5	coarse/h.c.	no	7.5	no
SMNK (RLB 85/74)	txp4	rt	23.5	26	fine	no	5.5	no
SMNK Hoe 8	txm1 or m2	rt	18.5	32	fine/coarse	no	8.5	no
SMNK Hoe 212	txm2	lt	17.5	27.5	fine/coarse	no	4.5	no
SMNK Hoe A	txm2	rt	6.5	27	fine	no	2.5	no
SMNK Hoe B	txm2	lt	23	26.5	coarse/h.c.	no	0	no
SMNK Hoe C	txm2	rt	21	33	fine/coarse	no	8.5	no

Tab. 2 - Microwear results. txm: maxillary molar; txp: maxillary premolar; rt: right; lt: left; h.c.: hypercoarse; Lg. pits: large pits; Punct. p.: puncture pits.

low-relief cusps, and instead proposed a new method. Earlier mesowear studies employing a ranked scale of single mesowear scores (e.g., Rivals et al., 2007; Croft & Weinstein, 2008; Rivals et al., 2009) essentially calculated or derived these scores from the individual cusp shape parameters recorded following Fortelius & Solounias (2000). In contrast to these earlier methods, Mihlbachler et al. (2011) obtain their mesowear scores according to a standard template with seven qualitative stages (0-6), which represent a gradient from high and sharp (0) to low and blunt (6). The template or "ruler" used consists of molds of representative hypsodont equid paracone cusps arrayed according to qualitative stage. Mihlbachler et al. (2011) assigned one of the seven scores to each analyzed paracone if the shape of this paracone was equally as sharp as or sharper/higher than the reference cusp of that score on the ruler. We have adopted this methodology herein, but also (preliminarily) recognize intermediate scores in 0.5 increments assigned if the observed cusp shape cannot unambiguously be assigned to one of the seven original steps but appears to fall in between two steps: 0.5, 1.5, 2.5, 3.5, 4.5, 5.5. The Mihlbachler et al. (2011) method has proven replicable amongst the three authors of this manuscript and effectively reduces inter-investigator scoring error. There is some controversy evident in recent studies concerning whether states such as low and sharp and high and blunt are possible due to normal attrition/abrasion processes (cf. Rivals et al., 2007, 2009; Mihlbachler et al., 2011). Since we did not observe such cases in our material for this and earlier studies (e.g., Wolf et al., 2010, in press), we cannot contribute to this issue here.

Mesowear scoring was undertaken on the original specimens and reviewed using high-resolution photographs as well as plaster casts of the original material. The calculated mesowear mean score for the Höwenegg hipparions following Mihlbachler et al. (2011), and the cusp relief and shape data observed following Fortelius & Solounias (2000) and Kaiser & Solounias (2003) were plotted using Excel 2007 for Windows. In addition, we calculated hierarchical cluster analyses to compare the mesowear results for Höwenegg *Hippotherium primigenium* with extant ungulates with known diets following both the Fortelius & Solounias (2000) and Mihlbachler et al. (2011) methodologies. We employed the ''conservative''classification (CONS) scheme of Fortelius & Solounias (2000) which treated doubtful cases as intermediate or mixed feeders. For the Mihlbachler et al. (2011) methodology, the data available for recent comparative taxa were transformed into scores by Mihlbachler et al. (2011) following the procedures described therein.

Microwear - Low-magnification stereomicroscopy microwear analysis was undertaken following Solounias & Semprebon (2002). The second enamel band of the P4-M3 paracone (or metacone, if necessary) was examined in all cases. Tooth enamel bands were cleaned, molded, cast and examined at 35x magnification. The average number of pits (rounded features) versus average number of scratches (elongate features) were assessed within a 0.4 mm square area for each individual under study. These observations were compared to a database constructed of extant ungulate taxa to determine the dietary categories of browser versus grazer versus mixed feeder (Solounias & Semprebon, 2002). We also noted whether gouges or puncture pits were present and whether there were more than four large pits present or absent per microscope field (within the 0.4 mm square area). Scratch texture was qualitatively scored as being either predominantly fine, predominantly coarse, or a mixture of fine and coarse types of textures per tooth surface.

RESULTS

Mesowear

Mesowear scores of Höwenegg *Hippotherium primigenium* could be obtained for eleven individuals. Only one score per individual was taken to avoid data inflation (Tab. 1). Following the Fortelius & Solounias (2000) methodology, we recorded the following results for the selected P4-M3s (after Kaiser & Solounias, 2003): 100% of the cusps are high, 18.2% of the cusps are sharp, and the remaining 81.8% are round; low or blunt scores were not observed (Fig. 1a). A hierarchical cluster analysis places the Höwenegg horse in close proximity to a number of extant fruit browsers (*Cephalophus natalensis* Smith, 1834 and *Hyemoschus aquaticus* Ogilby, 1841; Fig. 1b). The average score for Höwenegg *Hippotherium primigenium* following Mihlbachler et al.'s (2011) methodology is 1.09 with a range from 0 to 2. When we utilize our "half-step" methodology, the mean score is 0.95. In other words, Mihlbachler et al.'s (2011) method in our opinion slightly underestimates the sharpness and height of cusps by virtue of the fact that it does not observe 0.5 intermediate increments but rounds scores upwards (Fig. 1c). Using this method, the Höwenegg hipparion clusters with *Cervus canadensis* Erxleben, 1777, a high altitude (C3) grass-dominated feeder, *Odocoileus hemionus* Rafinesque, 1817, a browser, and *Tragelaphus scriptus* Pallas, 1766, a selective browse-dominated mixed feeder (Solounias & Semprebon, 2002; Fig. 1d).

Microwear

We were able to obtain microwear data for ten individuals. Fig. 2a plots the raw counts of scratches against raw counts of pits in relation to the morphospaces of browsers and grazers as established by Solounias & Semprebon (2002). Both the average (mean) of the counts for Höwenegg *Hippotherium primigenium* (17.9 scratches, 27.65 pits) as well as the values for the individual specimens are plotted (see Tab. 2). The majority of data points (seven individuals) cluster in between the browsing/grazing morphospaces, but largely in close proximity to the grazing morphospace (Fig. 2a). The other three individuals plot in the browsing morphospace as well as in the low scratch range (0-17 scratches), which results in a low scratch value of 30% (consistent with extant mixed feeders). Additional microwear features are given in Tab. 2. Four individuals show a fine scratch texture, four specimens have a mixed fine/coarse texture, and two teeth revealed a coarse/hypercoarse texture (see Fig. 2b). Gouges were only observed in one case, while six individuals showed a number of large pits; puncture pits, which are consistent with fruit browsing, are absent.

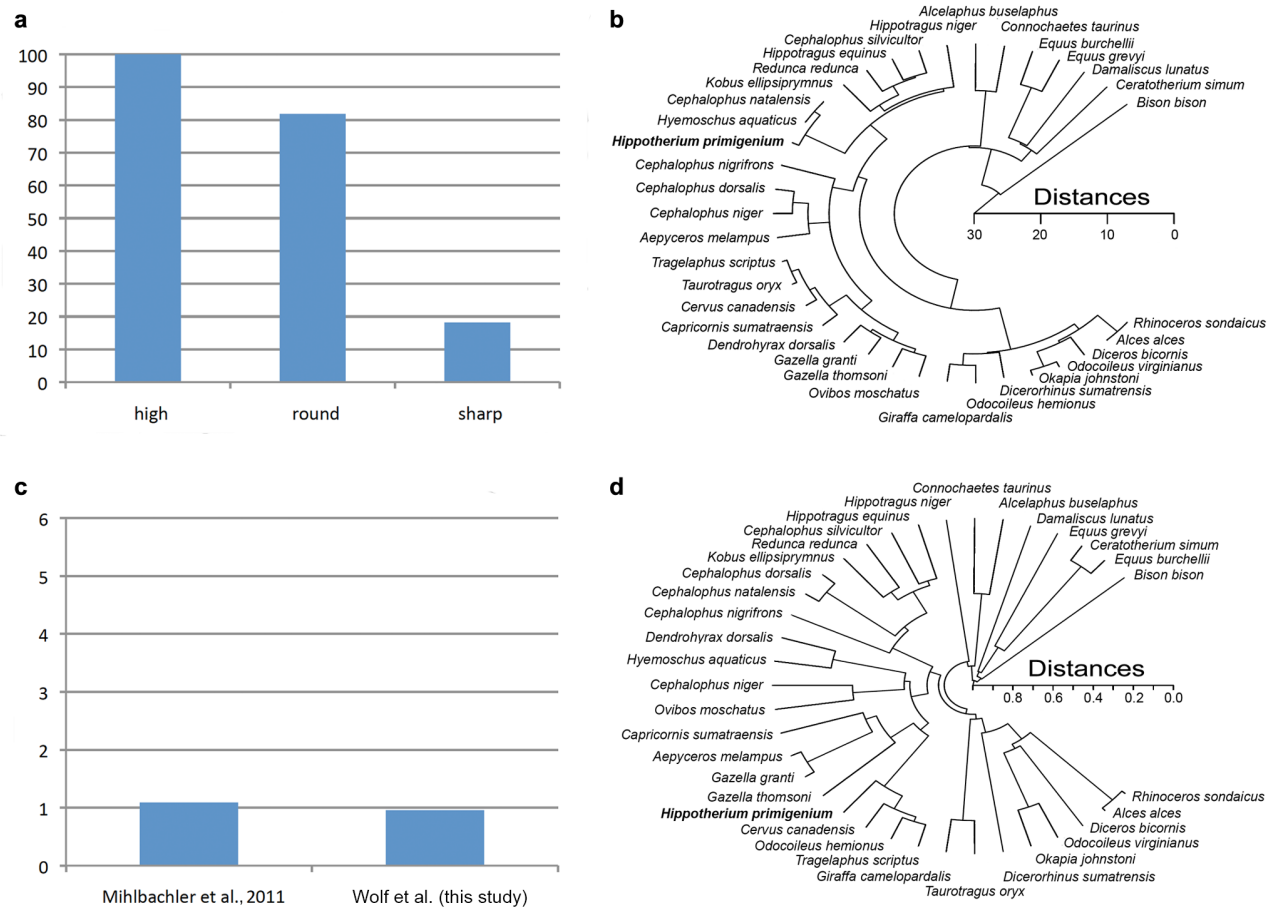

Fig. 1 - Results of the mesowear analysis. a) Percentages of high, sharp, and round variables of the Höwenegg population of *Hippotherium primigenium* following Fortelius & Solounias (2000) and Kaiser & Solounias (2003); b) cluster analysis of the result in 1a ranking the Höwenegg hipparion compared to extant ungulates with known diets; c) mean mesowear score according to the Mihlbachler et al. (2011) method and adjusted score recognizing half-steps (this study); d) re-calculated cluster analysis using the unadjusted score of 1c and known values for extant comparative data.

DISCUSSION

Both mesowear approaches employed by us, which are known to reveal a more long-term dietary signal than the microwear method discussed below (Fortelius & Solounias, 2000; Rivals & Semprebon, 2006; cf. Wolf et al., 2010), point to an at most moderately abrasive paleodiet of the Höwenegg horses (the mesowear in fact mainly constituting a measure of abrasion). By inference this also suggests a generally non-abrasive environment, i.e., low amounts of dust and grit ingested with the hipparions' food items (which is corroborated by the microwear results, see below).

More specifically, our cluster analysis using the original Fortelius & Solounias (2000) mesowear scoring methodology has Höwenegg *Hippotherium primigenium* clustering with certain extant fruit browsers, though it seems unlikely to us that *H. primigenium* was a fruit-dominated browser based on its gross tooth morphology and microwear results (see below). These results thus underscore the necessity of using several different paleodiet methodologies to obtain a more reliable interpretation of paleodietary preferences, and point to certain weaknesses of the Fortelius & Solounias (2000) method especially when used alone. However, it should be mentioned that *Celtis* fruits are very abundant in the Höwenegg sediments; it is therefore likely that the Höwenegg horse consumed a low-abrasion diet that occasionally also included fruits, even though this is not evident in the microwear signal.

The mesowear score of 1.09 (or, adjusted, 0.95) for Höwenegg *Hippotherium primigenium* following Mihlbachler et al. (2011) is most consistent with a browsing to browse-dominated mixed-feeding dietary signal and compares closely with North American brachydont equids such as *Hypohippus* (range of average scores = 0-2). North American *Cormohipparion* spp. (excepting *C. goorisi* MacFadden & Skinner, 1981), which represent the ancestral group for Old World *Hippotherium*, have a mesowear average range of 1.5-4, characterizing them as predominantly mixed feeders with a broad range of (generally more abrasive) diets (Mihlbachler et al., 2011). The results of our cluster diagram using preliminary extant comparative data and the non-adjusted value for the Höwenegg hipparion population shows that *H. primigenium* clusters with ungulates that habitually mix-feed with a dominant browse and/or low-abrasion (C3) grass diet (cf. Solounias & Semprebon, 2002).

In view of earlier studies on the paleodiet of Central European *Hippotherium* we recognize the potential for unwittingly interjecting observer bias in prior studies by recording and using scores of up to 8 tooth positions per individual (P4-M3 right and left sides; e.g., Kaiser, 2003, tabs 2 and 4), which weights the scores of those individuals favorably and may skew population dietary signals. In any case, Kaiser (2003) compared Höwenegg *Hippotherium primigenium* to the pene-contemporaneous population of *H. primigenium* from Eppelsheim, Germany, concluding that the two populations varied in the trophic regime they lived in as suggested by their mesowear variables in particular when the extended ("four-tooth method") is utilized; both statistical results for the original "one-tooth method" and the extended mesowear method (Kaiser & Solounias, 2003) are given, but the author considers the former less informative. His data supporting this conclusion were: Höwenegg (HO) had 100% high cusps (same as ours), while Eppelsheim (EP) had 97% high cusps; HO had 79% sharp cusps (versus 18.2% sharp and 81.2% round of our analysis), while Eppelsheim had only 16% sharp cusps using the extended mesowear method. Neither population had any frequency of blunt cusps. Results given for the one-tooth method are similar for Höwenegg, with slightly fewer sharp cusps (70%), while the Eppelsheim population had 100% high and round cusps using this version of the mesowear method (Kaiser, 2003, tab. 4).

In our sample we observe that the Höwenegg population has largely the same frequency of round and sharp cusps as the Eppelsheim sample rather than the Höwenegg sample as reported by Kaiser (2003) using both versions of the method, and this is at least in part due to differences in scoring cusp "sharpness" among observers. Through this study, as well as current studies on Siwalik and Ethiopian equids (e.g., Wolf et al., in press), we find that the Mihlbachler et al. (2011) mesowear method largely neutralizes this problem of inter-observer conflict by recognizing relative sharpness or roundness or bluntness as being gradational from highest and sharp (which would suggest dedicated grazing, cf. Mihlbachler et al., 2011) to absolutely blunt, or more dedicated browsing. Inter-observer deviation rarely exceeds one step on the mesowear ruler, which may not as strongly affect the overall result as would be expected from inter-observer disagreement when following Kaiser & Solounias (2003), which is recorded in fewer categories.

The microwear signal recorded by us suggests that Höwenegg *Hippotherium primigenium* consumed more grass than expected when considering only the results of our mesowear analyses. Only 30% of the microwear sample is in the low-scratch range, which places the Höwenegg *Hippotherium* into the mixed feeder range towards the more grass-dominated zone (Semprebon & Rivals, 2007). The overall rather fine scratch texture suggests grazing of C3 grass (Solounias & Semprebon, 2002). While the range of scratch/pit plot data points overlaps in part with the fruit browsing morphospace, more detailed microwear analysis did not show high percentages of large pits nor reveal any puncture pits, which would be typical of fruit browsing, and the pit count in the Höwenegg sample was also lower than would be expected of fruit browsers (Solounias & Semprebon, 2002). Despite the short-term nature of the microwear signal, this result makes the interpretation of a possibly fruit-browsing paleodiet of the Höwenegg horse after Fortelius & Solounias (2000) less likely than the mesowear result following Mihlbachler et al. (2011).

The disparities between the results of both mesowear methods and the microwear method, which would suggest a more grazing behavior than indicated by either one of the mesowear approaches indicating a less abrasive diet, may be explained by a generally low abrasive C3 grass diet of Höwenegg *Hippotherium primigenium* causing less abrasion than would be expected from a C4 grass diet. Future carbon isotope studies should aid in assessing this hypothesis. Since we believe that most Höwenegg fossils

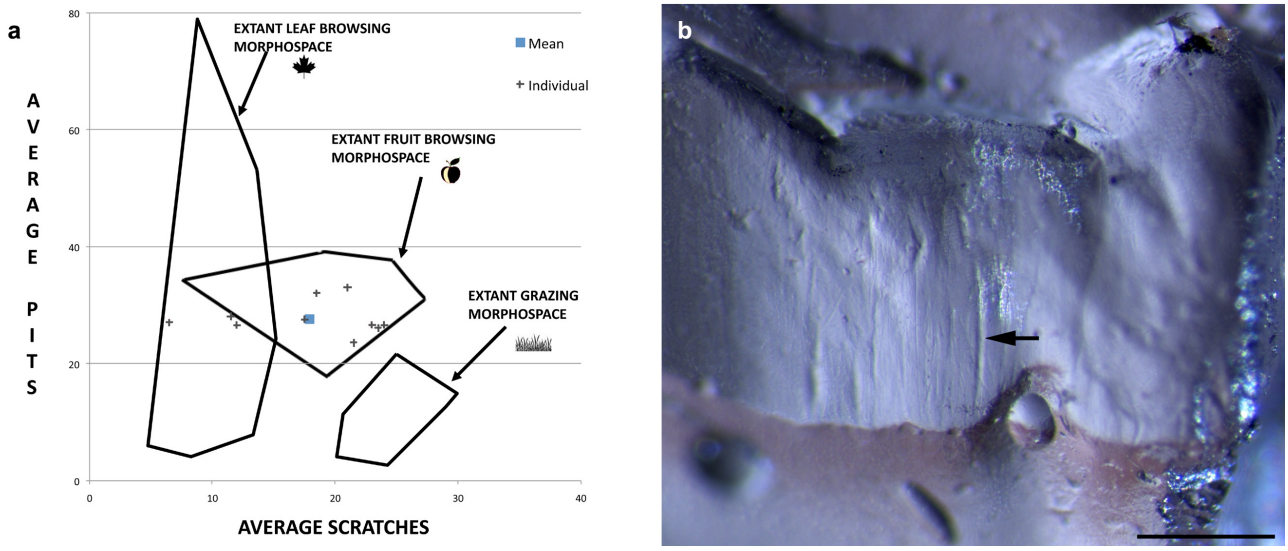

Fig. 2 - Results of the microwear analysis. a) Average counts of scratches vs. pits plotted for the Höwenegg *Hippotherium primigenium* individuals and the mean of this population, shown with respect to known browsing, grazing, and fruit browsing morphospaces; b) the microwear of one specimen as seen under the light microscope (HLMD Hoe M55-1; paracone, right maxillary M2); a hypercoarse scratch is marked by the arrow. Scale bar: 500 µm.

were deposited over a very short duration, it would also be possible that the single disparity we see in the hipparion assemblage reflects genuine dietary variability with grass being ingested only seasonally and only affecting the relatively short term microwear signal (Grine, 1986).

CONCLUSIONS

The Höwenegg *Hippotherium primigenium* was a primitive Old World hipparionine that lived in subtropical to warm-temperate mesophytic forests (Bernor et al., 1988). It had a mixed diet that included grass and browse and maybe hard endocarp fruits (such as *Celtis*). The high content of grass in the mixed diet is only evident in the microwear signal. This study underscores the importance of including light microscope microwear analysis alongside mesowear when evaluating paleodiet. We also find that the Mihlbachler et al. (2011) mesowear methodology assists in reducing inter-investigator error in mesowear scoring, especially the subjective evaluation of what constitutes "sharp" versus "round" cusps.

ACKNOWLEDGEMENTS

We are grateful to Oliver Sandrock and the staff of the Hessisches Landesmuseum, Darmstadt, Hans-Walter Mittmann and the staff of the Staatliches Museum für Naturkunde, Karlsruhe, and the administration of the town of Immendingen for access to the various Höwenegg collections. Matthew C. Mihlbachler and Nikos Solounias of the New York College of Osteopathic Medicine, New York Institute of Technology, generously provided us with a copy of their mesowear template. We would like to thank Lorenzo Rook of the Università di Firenze for translating the abstract into Italian. Spencer G. Lucas, New Mexico Museum of Natural History and Science, and two anonymous reviewers provided valuable suggestions for improvement of our manuscript. This research was supported by NSF grants EAR:0125009 to R.L. Bernor and BSC:0321893 to F. Clark Howell and Tim D. White (the Revealing Hominid Origins Initiative).

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Manuscript received 22 February 2012
Revised manuscript accepted 18 December 2012
Published online 30 December 2012
Editor Annalisa Ferretti